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Visual Optics: Accommodation in a Splash

Gannets are large seabirds that hunt fish from the air, making a plunge dive followed by active swimming pursuit of prey. A recent study shows that they convert from aerial to aquatic vision nearly instantly.

Thomas W. Cronin

One of the great sights in nature is a flock of wheeling gannets over the ocean hunting fish. These impressive birds, with wingspans approaching two meters, fold their wings as they sight their prey and plummet into the sea from heights of 10 or more meters like avian cruise missiles. The momentum gained from the plunge takes them well below the sea's surface, whereupon they turn to active swimming pursuit of the fish if the initial attack fails. Plunge-diving demands a suite of adaptations to direct the plunge, tolerate the impact, and transition from seeing and moving in air to subaquatic visual pursuit.

Many birds specialize in catching fish. Herons make a stealthy approach, wading in shallow water, sighting prey, and snatching it with a quick dart of the head and bill. Ospreys soar over bodies of water in search of food, and stoop to enter the water feet-first to grab their intended victims. Birds that hunt like these are not thought to have any special adaptations for underwater vision. Prey is detected and located from the air and the ambush attack gives no time for a change of plans once contact with the water is made. They just need to correct for image displacement of the target produced by refraction at the water's surface.

Other species of birds, like grebes, loons (divers), cormorants, and penguins are strictly submarine visual predators. Some float at the surface with their heads submerged, vigilant for passing prey which they then pursue underwater, powered by their feet. Penguins, on the other hand, perform the entire search, chase, and capture sequence on dives that can (in some species) exceed 200 meters in depth and nearly half an hour in duration. Their wings are modified as hydrofoils, so that they literally fly through water. Auks and puffins, too, fly underwater after prey, although unlike penguins, their stubby wings also enable a buzzy sort of flight between the nest and their foraging grounds. All these hunters obviously require good underwater vision.

The final group of predatory seabirds use the mobility and search coverage provided by flight to locate prey, and then enter the water to catch it. Shearwaters and albatrosses are outstanding fliers, but surprisingly they are also reasonably accomplished divers that pursue prey underwater [1]. Most dramatic, however, are plunge-divers like the gannets, terns, and brown pelicans, which use momentum gained from the high-speed dive to carry them to the depth of their prey. Terns, kingfishers, and brown pelicans are committed to impacting or netting a selected victim, much like the spearing behavior of a heron, and may not require specialized adaptations for underwater vision. But the gannets and boobies almost immediately undergo a transition to underwater pursuit, propelled by their wings to chase down fish that are missed if the momentum-driven submergence fails to connect. A team of ornithologists and vision scientists working with a New Zealand colony of Australasian gannets (Figure 1) has now found that these animals are capable of switching from well-focussed aerial to aquatic vision in less than 0.1 second — literally in the blink of an eye [2]. To understand how such a feat might be possible, we need to consider the special demands of amphibious vision.

Amphibious Eyes

Aquatic vision is no great challenge. After all, the first chordates to evolve lens eyes were already able to see in water. But every human, on first submerging his or her head in water, finds that it is impossible to see anything clearly. The problem for us, and all terrestrial vertebrates, is that the major refractive element in our eyes is the cornea, the eye's clear, anterior surface. Because the cornea has a spherical shape and separates media of two quite different refractive indices, air (refractive index ~ 1.0) and aqueous humour (refractive index ~ 1.33), it acts as a strong converging lens. Consequently, the cornea does most of the refraction required to form a sharp retinal image. Only about a quarter of the work is taken up by the lens itself, which also performs the fine and adjustable focusing, the process called accommodation. When the eye is submerged, the corneal refractive power is lost, as the refractive index of water, whether seawater or fresh, is very similar to that of the biological fluids filling the eye. The power of the lens is completely inadequate to

Figure 1. A trio of Australasian gannets, *Morus serrator*, hunting fish.
These birds are searching for fish off the coast of New Zealand. The bird in the center has just initiated a dive by lowering its head and inverting its body in preparation for the plunge. Photo credit: Fabio Piccinato and Ticiana Fetterman, ©Takapu Research Project; used with permission.

pick up the required slack, and the resulting image falls far beyond the retina — hence the perception of extreme blurriness. This type of focus, behind the retina, is called hyperopia.

Eyes specialized to see in water do not use corneal focusing at all — the lens assumes the entire function of forming a sharp image. Obviously, such a lens has to be far more powerful than that of a terrestrial eye, and the required power is gained both by having a spherical shape (unlike the flatter, lozenge-shaped lenses of terrestrial eyes) and a carefully shaped internal gradient of refractive index that decreases with the distance from the lens's center (see [3] for an authoritative discussion of lens eyes on land and in water). Aquatic eyes, however, generally fail in air: being spheres themselves, their corneas are curved; on encountering air on their outer surface, their refractive power comes back into play and is added to the lens's, thus focusing images well in front of the retina (a condition termed myopia).

Despite the optical challenges, eyes of some animals incorporate mechanisms for truly amphibious vision. Some of these are compromises, giving excellent vision in one medium and acceptably degraded visual quality in the other. Examples are flattening the curvature of the cornea, seen in many marine mammals and aquatic birds. By increasing the cornea's radius, its power is reduced in air, providing a moderately myopic, but still acceptable image. Another possibility is to shrink the size of the pupil by closing down the iris. A reduced pupillary aperture increases the eye's depth of field, so that both near and distant objects can be imaged fairly clearly. This improves both hyperopic and myopic images, permitting the eye to retain some function in the 'wrong' environment. Remarkably, some human populations that forage underwater use this tactic to improve aquatic vision markedly [4]; the ability is probably learned with experience. Birds, however, may be the only living vertebrates that have truly excellent amphibious vision. Explaining how this is possible requires an understanding of how avian eyes accommodate.

Avian Mechanisms of Accommodation

The study of how bird eyes form images has a long and distinguished history, dating back to the very early years of the 19th century [5]. It is fair to say that, as a whole, birds use a greater variety of focusing mechanisms than other vertebrates, employing not only changes in the overall curvature and position of the lens, but in some species designs that also involve the cornea or the iris [5,6]. Having this diversity of functional systems available has enabled the evolution of high-quality aquatic and amphibious vision.

Birds evolved on land; their eyes are fundamentally terrestrial eyes (Figure 2). Like those of mammals, their eyes typically have a domed cornea, a somewhat flattened lens acted on by a ciliary process, and a roughly hemispherical retina. They differ in having a ring of scleral ossicles surrounding the region of the iris and often a highly muscular iris, sometimes incorporating independent central and peripheral sets of muscle. Two routes to avian amphibious function are diagrammed in Figure 2. In the case on the right, adopted by albatrosses, penguins, and probably other seabirds, the lens is nearly spherical and the cornea flatter to reduce its contribution in air. Any required refractive adjustment is done by the lens. This design is not unique to birds; similar modifications are seen in seals and otters. The other amphibious design, on the left in Figure 2, is a strictly avian innovation. It relies on the strengthening ring of scleral ossicles, the outer muscles of the iris, and the powerful ciliary body to squeeze the lens and shove it forward through the pupillary aperture when the eye enters water. The resulting bulge in the lens's anterior surface grants it increased refractive power, making up for the loss of corneal refraction. This mechanism is documented in diving ducks [6] and likely is used in cormorants [7] and other diving birds. It also operates less dramatically in penguins, which similarly need to deal with the need to make up for the lost corneal power, although the flattened cornea lessens the required change [8]. But what about gannets?

Amphibious Vision in Australasian Gannets

In their work with Australasian gannets, *Morus serrator*, Machovsky-Capuska's team [2] videotaped birds foraging naturally at sea, and captured animals for visual measurements at the aptly named Cape Kidnappers colony on New Zealand's northern island. Corneas were measured using a technique that quantifies patterns of light reflected from the corneal surface, while the refractive state of the eyes of animals both in air and underwater was measured by another reflective method, infrared video retinoscopy [9]. The animals were unharmed by these noninvasive techniques and were immediately released after being measured. Results suggest that the corneas of these birds are not unusually flattened. Retinoscopy nevertheless revealed that the eyes are

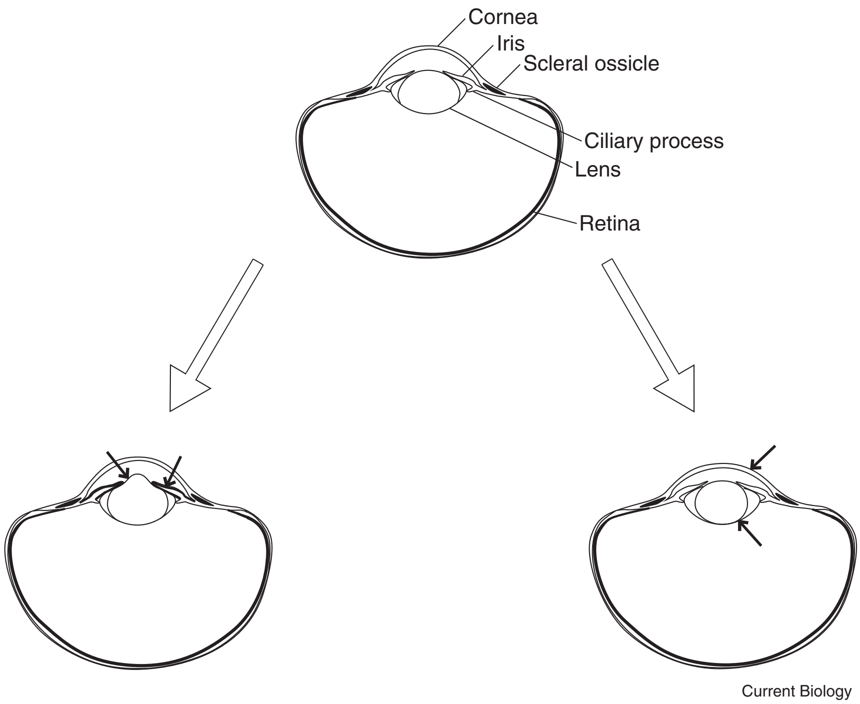

Figure 2. Two evolutionary paths leading to amphibious vision in birds.

The top figure diagrams a typical avian eye, indicating the components important in imaging. Light enters the eye through the cornea, passes through to the lens via the aperture formed by the iris, and is focused onto the retina. Accommodation is achieved using the ciliary muscle, in the ciliary process connecting the outer margin of the lens to the rigid outer coat of the eye. The rigidity is increased by the presence of a ring of intraocular bones, the scleral ossicles, surrounding the eye below the cornea. In birds like penguins, the power of the cornea is reduced by having a flatter curvature; the lost power is regained with the use of a more spherical lens (right side, with the modifications indicated by arrows). Diving ducks, and probably gannets, employ a different mechanism, diagrammed on the left. They use the ciliary muscle to pull the lens forward, and the muscles of the thicked iris force the lens's anterior surface into a projection with a very short radius (and thus increased refractive ability), again indicated by the arrows (drawing by Judy Rubin).

properly focused in both air and water. Remarkably, the switch from aerial to excellent aquatic vision was complete before the first clear video frame was acquired after submergence, in less than 100 milliseconds. The animal tolerates its high-speed penetration of the water's surface so well that it can sight its prey immediately and initiate pursuit as soon as the momentum of the plunge dissipates. Its visual abilities provide remarkably successful underwater pursuit predation — while only about half of the initial plunges lead to prey capture, over 90% of pursuits are successful, and birds not uncommonly capture one fish in the plunge and another during pursuit.

The speed of the transition from aerial to aquatic vision is almost certainly achieved by actively reshaping the lens against the iris (left path in Figure 2), although direct evidence for this is still lacking. Whether or not gannets or other amphibious birds can accommodate for sharp imaging of prey sighted at different distances underwater is also unknown. Such an ability should be advantageous for high-speed, visually directed pursuit, but it is apparently lacking in dolphins and possibly other marine mammals [10]. In addition, underwater vision requires rapid adaptation to a dimmer, bluer light environment than in air. As extremely successful hunters, gannets obviously are able to cope with these instantaneous changes in their visual world.

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RNA Interference: Systemic RNAi SIDes with Endosomes

Systemic RNAi, the intercellular spreading of RNAi silencing, requires SID-1 and SID-3 to import silencing signals in *Caenorhabditis elegans*. How are these signals exported? SID-5, an endosome-associated protein, is a candidate for the job.

Christian E. Rocheleau

RNA-mediated interference (RNAi), the process of gene silencing through the introduction of double-stranded RNA (dsRNA), was first discovered in the nematode *Caenorhabditis elegans* [1]. One of the phenomena